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Heterochrony in Human Evolution: The Case for Neoteny Reconsidered

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ABSTRACT This paper reviews the evidence for the claim that *neoteny,* or morphological juvenilization resulting from dissociation and retardation of ancestral rates of shape change, has played a key role in human evolution. Accepted categories and processes of heterochrony are reviewed, and the available data on human growth, variation, and evolution are analyzed in light of expected results. Relatively weak concordance with predictions is found. Mistakes of fact and interpretation fall into several categories, including 1) confusion of neoteny with paedomorphosis resulting from other heterochronic processes; 2) conflation of growth prolongation in time with morphological shape retardation; 3) failure to move beyond superficial shape similarities to underlying homologous growth processes and patterns; 4) failure to identify a paedomorphic basis for key anatomical novelties in human evolution; and 5) establishing an essentially untestable framework for analysis of the hypothesis. Key areas that might contribute new data to this debate are discussed, particularly the genetic and epigenetic control of the covariation of morphology and development during ontogeny and evolution. The primary reasons that arguments in favor of neoteny in human evolution have persisted probably relate to anthropocentric factors and the search for a single basis for the important morphological and behavioral transformations characterizing our lineage.

The claim that *neoteny* has played a central role in human evolution has spawned one of the most persistent and vexing debates in physical anthropology over the past century. Treatments ranging from focused morphological investigations to major theoretical treatises have been produced, but little in the way of consensus and resolution has emerged. How, therefore, can we justify yet another review of this problem? I attempt such a justification along several lines. First, the volume of ink spilled over this topic is hardly evenly divided between pro and con—advocates outnumber detractors, at least in the published literature of the past several decades. I will argue here that there are numerous inconsistencies in these arguments that have never been pointed out, sufficiently stressed, or synthesized. Second, there is a considerable amount of new information germane to this issue that has been produced in the decade since the last major review of human neoteny, that by Gould (1977). Most of this information comes from outside the study of human evolution, but it is directly relevant to the question of human neoteny nonetheless. Finally, rather than simply attempting to offer a resolution or the "final word" on this topic, I will try to point out the areas of critical knowledge that are lacking and that would contribute to a better understanding of this and related issues. Because most previous authors have strongly and defensively

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advocated a particular view in this debate, there has been relatively little consideration of the types of new data that might hasten resolution of the neoteny question.

There is another reason why the neoteny debate is of central importance to physical anthropologists. The literature on this topic provides exceptional insights into the historical and philosophical influences on anthropologists and other scientists as they reconstruct human evolution, and thus stories of how and why we came to be as we are. These significant issues have been analyzed by previous authors, particularly by Gould (1977), and therefore I will not attempt to treat them further here. The reasons that particular theories and hypotheses are rejected and discarded are complex. I accept that data are normally collected and interpreted in light of particular theoretical orientations and that major shifts in theories or models are often not the simple result of the gradual accumulation of empirical data (Gould, 1977). But I do not view the issue of human neoteny as any such major theoretical construct, our normal and even understandable anthropocentrism notwithstanding. The significant theoretical context within which this debate must be analyzed is not at issue here. That context involves fundamental questions such as the relationships between ontogeny and phylogeny, the bases of morphological integration and covariation, and the evolution of morphology in relation to life history (e.g., timing) and ecological factors. That context is firmly established as the study of *heterochrony* in modern evolutionary morphology owing to the work of de Beer (1958), Rensch (1959), Gould (1977), Wake (1982), and many others. Although the debate over human neoteny may have played a significant role in the erection of this theoretical structure (and the downfall of previous ones), a modern consideration of this issue must carefully analyze the data of human development, variation, and evolution in light of the now-established theoretical framework. Heterochrony, or changes in morphology resulting from shifts in the rate or timing of ancestral developmental patterns, has undoubtedly played a central role in the evolution of humans, as in all other lineages (how could it be otherwise, given that phylogeny is literally a chain of modified ontogeny?). What is at issue is whether a *particular* heterochronic process, *neoteny,* has played a central role in human evolution and how we should go about testing this claim.

BACKGROUND TO HETEROCHRONY

A point often not fully appreciated is that the value of a heterochronic approach to morphology lies primarily in its elucidation of 1) the integration of many particular features, which may covary as the coordinated result of one or several underlying developmental processes and selective foci; and 2) morphological shifts that may secondarily result from changes in developmental timing, such as truncation or extension of growth periods. Any particular morphological feature may be described using traditional or novel categories and processes of heterochrony, since it is very difficult to envision a feature that is not the product (however transformed) of shifts in the rate and timing of ancestral developmental patterns. Moreover, it would hardly be very enlightening to compare the adult and developmental morphologies of two species to find that there are 17 key differences, and then proceed to fish through the seemingly bottomless chest of heterochronic jargon to come up with 17 developmental processes tagged to these changes. It would, however, be very informative and significant if 12 of those differences could be interpreted as an integrated result of a particular developmental process. It would be better still if we understood both the genetic and epigenetic bases of this process of transformation and the relevant selective forces and ecological contexts (see Shea, in press, for further discussion). There can be no simple recipe for determining when a heterochronic perspective is informative and when it decays to descriptive pedantry, but factors such as morphological covariation, links to known developmental processes, and clear concordance with predictions are several useful guidelines that we will return to in subsequent discussion.

Synopsis of current terminology

Anyone undertaking a critical review of the neoteny hypothesis of human evolution must carefully work through the currently accepted terminology of the *processes* and *results* of heterochrony, since it will become clear that a significant component of the misinterpretation in the history of this debate involves a failure to appreciate these distinctions. The following synopsis coincides closely with the fruitful revision of de Beer's (1958) categories proposed by Gould (1977), with the exception of several changes and additions suggested by me (Shea, 1983a). I continue to utilize the "clock models" of Gould (1977), rather than the more formalistic approach of Alberch et al. (1979), since changes in three parameters (size, shape, timing) can be more easily envisioned with the clocks. The primary quantitative basis of heterochrony, at least in studies of postnatal development, is growth allometry (Shea, 1983a).

Figure 1 outlines the six primary processes of heterochrony, grouped into resultant morphological categories of *paedomorphosis* (retention of ancestral juvenile characters or shapes by later ontogenetic stages of descendants), and *peramorphosis* (extension beyond the ancestral adult characters or shapes, i.e., repetition of ancestral adult stages in embryonic or juvenile stages of descendants—cf. *recapitulation* of Gould, 1977). A key element in Gould's (1977) synthesis is the separation of underlying processes from morphological results, combined with the realization that comparable or identical morphologies may result from disparate processes reflecting fundamentally different selective and ecological causes. Table 1 summarizes the processes, morphological results, and aspects of underlying allometries, rates of growth-in-time, and life history features for analysis of heterochrony. The following definitions are taken directly from Gould (1977:250–262) and Shea (1983a).

Figure 1A shows paedomorphosis via rate hypomorphosis. Ancestral rates of total weight growth per time are reduced, while patterns of allometry and duration of growth remain unchanged. Descendant adults are smaller, with juvenilized morphology (via ontogenetic scaling) and no change in growth duration.

Figure 1B shows paedomorphosis via time hypomorphosis (or progenesis). Ancestral rates of total weight growth per time remain unchanged, as do patterns of allometry, but the duration of growth is truncated in time. Descendant adults are smaller, with juvenilized morphology (via ontogenetic scaling) and a shorter duration of growth.

Figure 1C shows paedomorphosis via neoteny. Ancestral patterns of allometry are dissociated and retarded, so that shape change does not proceed as far and descendant adults are juvenilized in morphology. Descendant adult size and duration of growth remain unchanged.

Figure 1D shows peramorphosis (recapitulation) via rate hypermorphosis. Ancestral rates of total weight growth per time are increased, while patterns of allometry and duration of growth remain unchanged. Descendant adults are larger, with peramorphic morphology (owing to ontogenetic scaling and allometric extrapolation) and no change in growth duration.

Figure 1E shows peramorphosis via time hypermorphosis. Ancestral rates of total weight growth per time remain unchanged, as do patterns of allometry, but the duration of growth is extended in time. Descendant adults are larger, with a peramorphic morphology (owing to ontogenetic scaling and allometric extrapolation) and an increase in growth duration.

Figure 1F shows peramorphosis via acceleration. Ancestral patterns of allometry are dissociated and accelerated, so that shape change progresses further, and descendant adults are peramorphic in morphology. Descendant adult size and duration of growth remain unchanged.

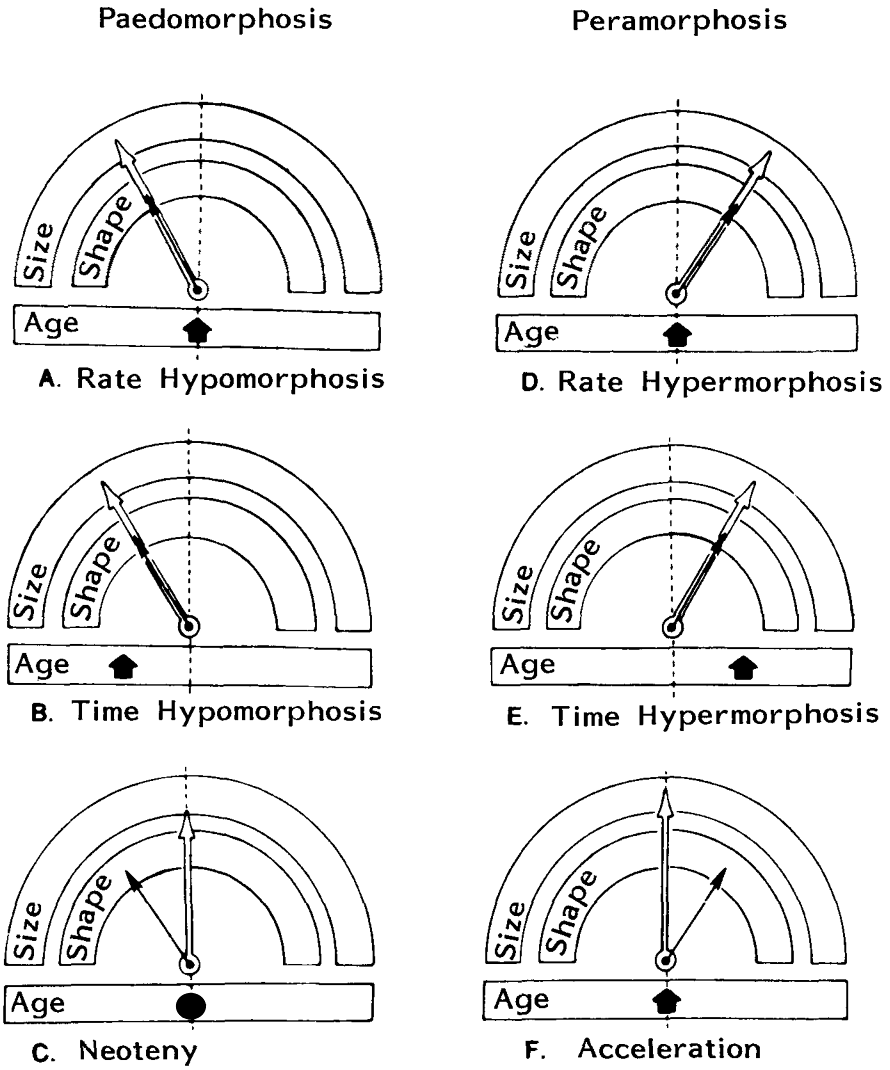

Fig. 1. (After Gould, 1977; Shea, 1983a.) The primary categories and processes of heterochrony, based on Gould's three-parameter clock models. The baseline or ancestral condition for the three "hands" of the clock (size, shape, and age) is given by the vertical dashed line. Heterochronic transformations are summarized by the deviation of the hands from this position. Ontogenetic scaling in a comparison of bivariate or multivariate growth allometries provides a metric test of whether size and shape vectors remain unchanged (as in hypo- and hypermorphosis) or are dissociated (as in neoteny and acceleration). See text for definitions and additional discussion.

Neoteny in Bermudian land snails—a case study

Gould's (1968, 1969, 1977) work on evolutionary transformations in land snails of the Bermudian Pleistocene provides one of the classic examples of heterochrony via neotenic paedomorphosis. Additional details on developmental patterns and ecological context can be found in these citations; here I am particularly concerned with this case as a clear example of a relatively complete neotenic transformation of multiple morphological features, as specified above.

Gould (1968, 1969, 1977) demonstrated that at least four times during the Pleistocene a central stock of the land snail, *Poecilozonites bermudensis zonatus,* gave off strongly paedomorphic descendants. These paedomorphs were the same size as the ancestral adult snails and presumably had developmental periods of the same duration. However, the ancestral patterns of shape change in shell color, thickness, and external form (i.e., spire, aperture and umbilicus shape) were strongly dissociated and retarded, such that "... all characters were affected; the paedomorphic shells are scaled-up replicas of early ontogenetic stages in the main lineage" (Gould, 1977:276). Figure 2 illustrates the widespread paedomorphosis via neoteny using photographs of actual specimens and a multivariate analysis of seven ratios of shape change.

This example is one of the clearest cases of neotenic paedomorphosis yet described in terms of the fit with predicted changes in size, shape, and developmental timing. Coordinated dissociation and retardation affect shape trajectories of numerous features, while ancestral developmental timing and terminal size remain unchanged.

Modern humans—a hypothetical case

Let us envision for illustrative purposes that a small group of humans colonizes a distant planet and over the course of the next several hundred thousand years evolves into a strongly paedomorphic form via neoteny. Developmental bases and selective scenarios aside in this hypothetical example, a fairly detailed consideration of what the derived morphology and life history pattern would resemble will help clarify some of the ensuing arguments in this paper. For the sake of clarity, I will also present hypothetical transformations along the various other heterochronic pathways outlined above. In these hypothetical examples, the transformations are assumed to be both *pure* (only the single heterochronic process involved, not mixing of various processes), and *complete* (basically the entire body affected, and different portions affected comparably in allometric terms). In a sense, we are quite literally describing the expected human results in a case paralleling the Bermudian land snail example.

Figure 3 presents a well-known schematic of human ontogeny that can be utilized to discuss the derived morphology of our neotenic descendants. This figure summarizes some of the primary changes of size and shape that characterize human ontogeny, such as relative decrease in head size and relative increase in lower limb length. Figure 4 maps the six major heterochronic processes presented in Figure 1 and Table 1 onto human growth trajectories and illustrates ultimate morphologies as well as specific size, shape, and timing changes. Figure 4C illustrates the derived morphology of our neotenic descendants. In essence, such descendants would first of all be the same size as adult extant humans, and they would become sexually mature and cease growth at approximately the same time as we do. Their ontogenetic trajectories of shape change would be dissociated and retarded, so that a strongly paedomorphic morphology would result. The changes in trajectories that are linear in a logarithmic and allometric sense would be straightforward. Positively allometric trajectories yielding relative enlargement in adults of the ancestral group would exhibit lower slopes so that descendant adults would be characterized by relatively smaller such structures, just as in juveniles of the ancestors. Lower limbs in our hypothetical human example fit this category—paedomorphic descendant adults would have relatively shorter lower limbs than ancestral adults, although at the same body size. Negatively allometric trajectories yield relative diminution of structures in the adult, so our descendant adults would exhibit a relative enlargment of such features compared to ancestral adults, thus resembling ancestral juveniles. Overall skull size, reflecting the postnatal negative allomety of the brain and perhaps also the face, is such a feature in this example (see Fig. 4C). In sum, these derived humans would age like us, look like us in overall body size, but resemble our juveniles in terms of bodily proportions.

Paedomorphic humans produced not by neoteny but by *time hypomorphosis* (the

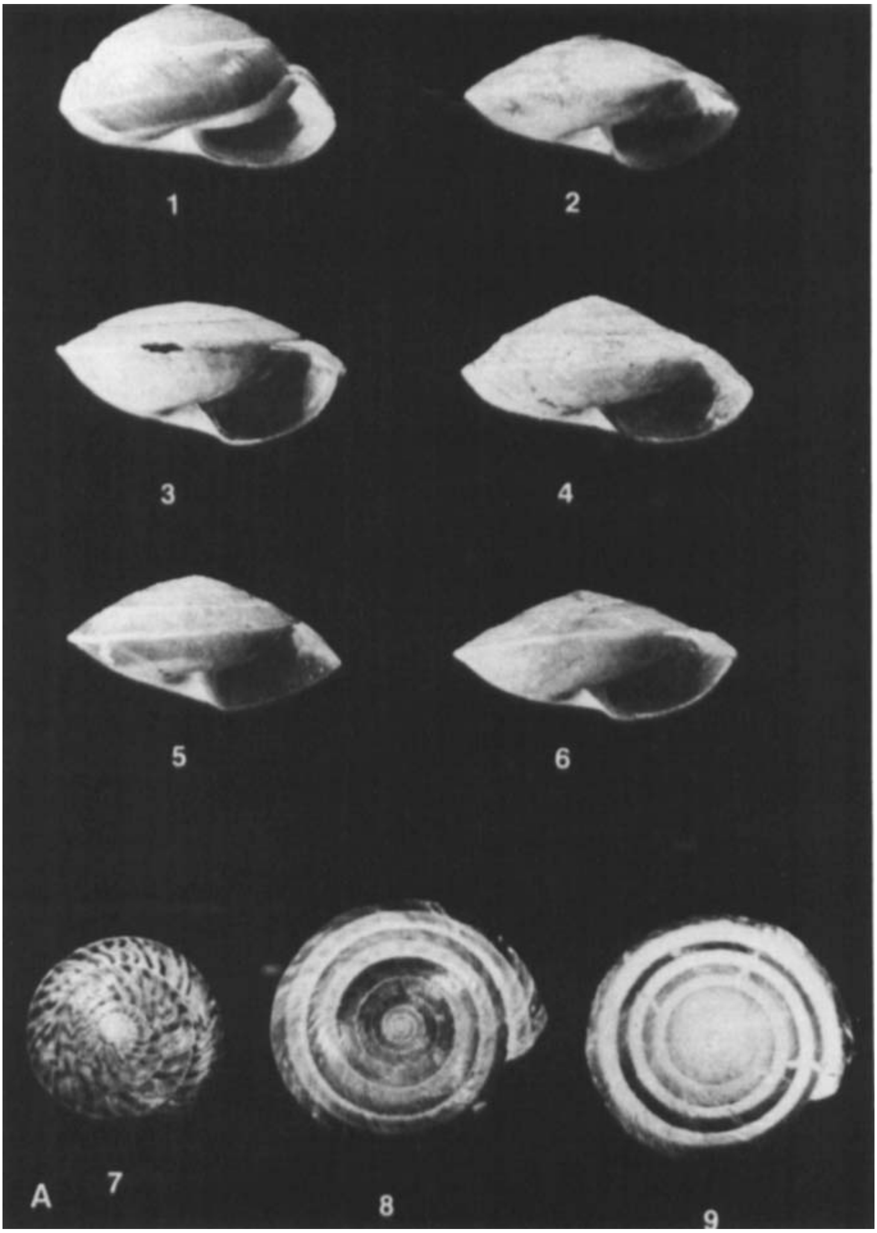

Fig. 2A.

Fig. 2. (From Gould, 1977.) Paedomorphosis via neoteny in land snails (*Peocilozonites bermudensis*) of Bermuda. **A** illustrates shell form in **1**) the normal adult non-paedomorph (length = 19.5 mm); **2**) the juvenile (11.5 mm) of the normal form *enlarged to the same size as its adult form in* 1; **3–6**) four independently evolved adult paedomorphs (lengths of 22.2, 21.5, 20.2, and 23.0, respectively). The bottom three shells (**7–9**) simply illustrate that the adult paedomorphs retain the juvenile pattern of non-coalesced color bands (as in **7**), in contradistinction to the normal adult coalesced pattern. In **B,** results of a multivariate morphometric comparison utilizing seven shape ratios reveal that adults of a paedomorphic group (P) cluster with the juveniles (Y), as opposed to the adults (A), of a non-paedomorphic population.

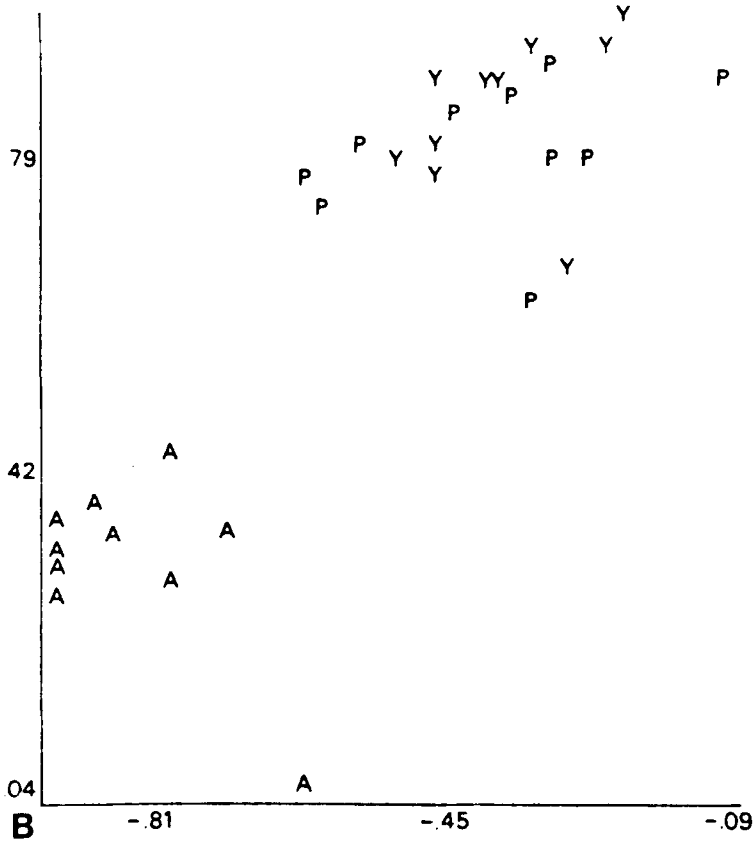

Fig. 2B.

progenesis of Gould, 1977, and some earlier authors) would be easily distinguishable from those just described. First, they would resemble juveniles in overall size as well as proportions, for their ontogenetic allometries would have been simply truncated in duration of growth and ultimate size attained, rather than "pulled apart" and retarded. These morphs are illustrated in Figure 4B, and they would quite literally be ancestral humans that ceased growth and matured inordinately early. Morphologically indistinguishable from these would be descendant paedomorphs produced by *rate hypomorphosis* (Shea, 1983a). Such adults would be in the size and proportion range of ancestral juveniles, but they would take as long to mature and cease growth as the ancestral adults, i.e., their ontogenies would be truncated only in size attained, and not duration of growth. Needless to say, they would exhibit a slowing or retardation of growth, but here we refer to overall *growth in body weight,* and not a dissociation of underlying allometric trajectories with a retardation of *allometric shape change,* as in neoteny. In other words, the way to distinguish between neoteny and rate hypomorphosis is, first, to compare final adult size attained (being smaller in rate hypomorphosis) and, second, to compare underlying growth allometries (being the same, or ontogenetically scaled, in rate hypomorphosis). The hypothetical new humans produced by rate hypomorphosis are illustrated in Figure 4A.

The processes yielding peramorphosis are parallel to those just reviewed. Peramorphosis via acceleration would result in a descendant of comparable size and duration of growth, but shape change relative to overall size would be accelerated

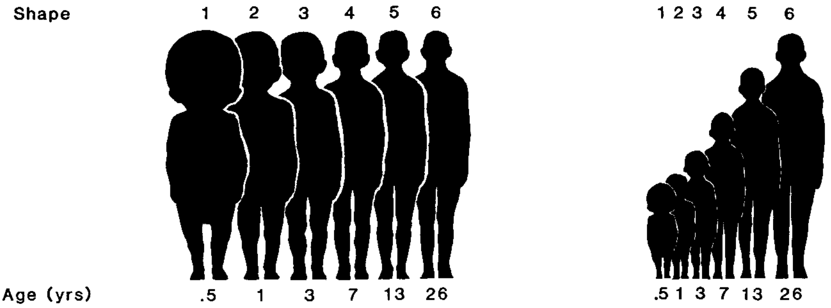

Fig. 3. Schematic illustration of the primary size, shape, and age changes characterizing human ontogeny. Shapes are coded from 1 to 6, with appropriate ages also given. The left panel dramatically illustrates some primary shape changes during human growth by reducing all stages to a common size. The right panel illustrates these same shape/age stages but at their appropriate total sizes.

(Fig. 4F). Relative head size would be even smaller and relative lower limb length would be even longer than in extant adults. Rate and time hypermorphosis would both yield giant descendants whose peramorphic shape results from an extension (ontogenetic scaling) of normal growth trajectories. In the former case, the duration of growth would be as in ancestral humans (Fig. 4D), whereas in the latter situation, ontogeny would be greatly extended in time (Fig. 4E). Thus, a simple transformation owing to time hypermorphosis would be produced by a lengthening or prolongation of ontogeny (based on one or more of the various growth periods).

THE EVIDENCE

In the following subsections, I review some of the primary inconsistencies and errors of fact and interpretation that have characterized the debate over human neoteny. My discussion is focused on examples representative of reasonably discrete types of arguments and errors, rather than attempting an exhaustive review. In a real sense, this section may be thought of as a test of the predictions of the preceding outline of heterochronic processes and results using the basic data of human development, variation, and evolution, save that in this case we are viewing extant adult humans (rather than transplanted extraterrestrials) as the product of a purported neotenic transformation.

Size-related shape changes

Many features frequently cited as evidence of human neoteny are arguably paedomorphic, yet they result from rate and/or time hypomorphosis and not the process of shape dissociation and retardation, which is characteristic of neoteny. These features predominantly apply to discussions of modern human intraspecific variation (i.e., between sexes or groups), since there is little evidence to suggest that we are the dwarfed descendants of giant hominids (more on this below). These features figure most prominently in the discussions and lists given by Montagu (1962, 1974, 1981), although many others have cited examples of this type, and such features in fact make up a significant portion of those frequently taken as providing good evidence for neoteny.

A simple reduction in overall body size will bring about pervasive and allometrically coordinated juvenilization, unless accompanied by fundamental dissociations of baseline patterns of relative growth. This will occur whether the decrease in terminal body size results from rate hypomorphosis or time hypomorphosis (progenesis) (Shea, 1983a). Therefore, the package of morphological features distinguishing human females from males given by Montagu (1981) as evidence for general human neoteny and its exaggeration in the female is misinterpreted. Small faces, reduced cranial sinuses, decreased cranial robusticity and cresting, relatively larger brains, and other such proposed features are a direct result of the

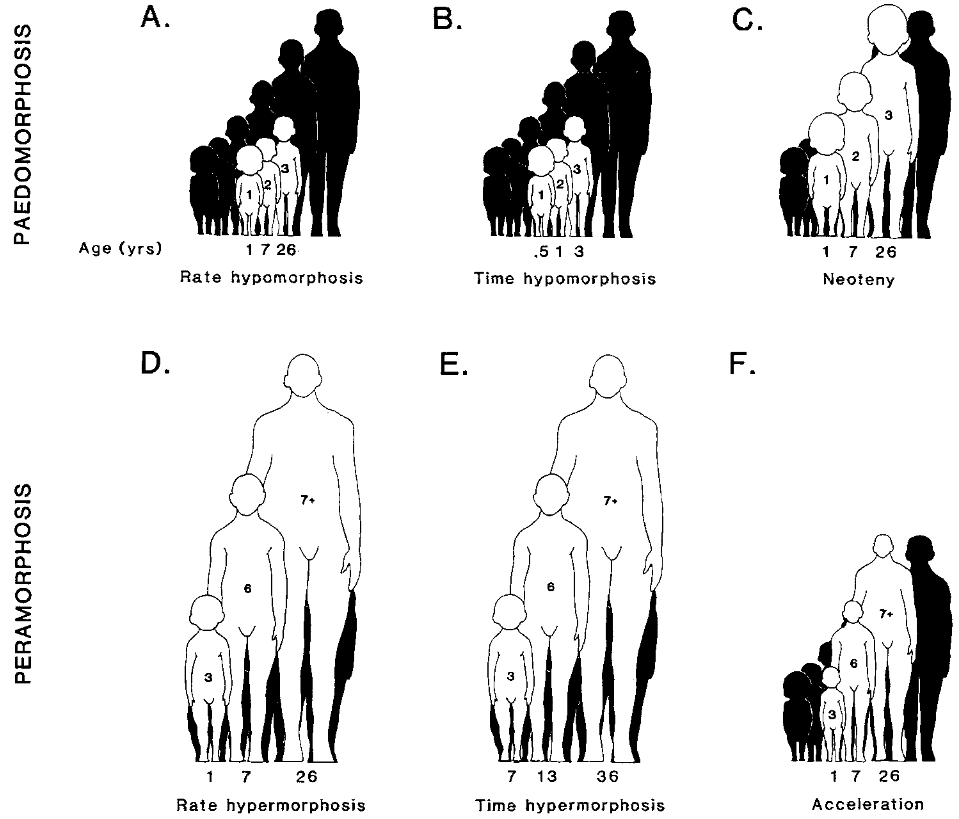

Fig. 4. Hypothetical heterochronic transformations based on modern human development. The size, shape, and age pattern of human growth depicted in Figure 3 is used for comparative purposes (solid background) to illustrate hypothetical heterochronic transformations. These (A–F) match the sequence from Figure 1 using the abstract clock models. For the sake of clarity, only three growth stages in the transformed case are illustrated. Age information is provided below the transformed figures, and the shape coding from the baseline sequence is used for comparison (a value of 7 + has been used to quantify peramorphic shape). Overall size is accurately depicted, so the transformed adult can be compared to the baseline adult. See text for additional discussion.

female's smaller size in sexually dimorphic humans. However, a truly neotenic female (relative to the male and for this example the presumed ancestral adults of both sexes) would be as large as the male but would still exhibit such a paedomorphic suite of features. This is not the case in human females.

A comparable argument must be made concerning the long debate by Bolk (1929), Drennan (1931), Keith (1949), Montagu (1962, 1981), and many others, including even Gould (1977), over neoteny as a process of differentiation among modern human populations or races. Features extracted from a compilation by Montagu (1962) and illustrative of the general failure to control for simple allometric effects of smaller body size include small face, small mastoid processes, small cranial sinuses, bulging forehead, relatively large brain, larger braincase, brachycephalism, lack of brow ridges, and greater gracility of bones. Montagu even lists small body size as a neotenic feature here, although this is certainly not a prediction of neoteny given the heterochronic profile outlined above. Furthermore, it is frustrating, although entirely characteristic of the many factual and interpretive contradictions that riddle this debate, to find that Gould (1977) lists *large* body size as primary evidence for neoteny in human evolution. Yet there is no

TABLE 1. A summary of the primary heterochronic processes, their morphological results, underlying changes in size, shape, and timing parameters, and concordance with the predictions of ontogenetic scaling or dissociation of growth allometries[1]

Heterochronic process	Morphological result	Size, shape, and timing (age) change	Allometric trajectories
Rate hypomorphosis	Paedomorphosis	Size/shape[2] decrease	Ontogenetic scaling
Time hypomorphosis	Paedomorphosis	Size/shape[2] and age decrease	Ontogenetic scaling
Neoteny	Paedomorphosis	Shape[3] decrease	Dissociation
Rate hypermorphosis	Peramorphosis	Size/shape[2] increase	Ontogenetic scaling
Time hypermorphosis	Peramorphosis	Size/shape[2] and age increase	Ontogenetic scaling
Acceleration	Peramorphosis	Shape[3] increase	Dissociation

[1] See text for additional discussion and compare to Fig. 1 and Fig. 4.

[2] Size/shape here refers to a particular allometric trajectory; increase and decrease simply refer to the extension and truncation of this growth trajectory.

[3] Shape here refers to proportion changes with no necessary concomitant size changes, i.e., underlying allometries are broken or dissociated to produce new shape values at common size values.

necessary expectation regarding size change in neoteny, and in fact in a pure neotenic transformation, size is predicted to remain the same. It is clear that many of the morphological features offered as evidence of neotenic differentiation among human groups are the simple allometric consequence of differences in overall or regional body size.

Human pygmies provide an excellent case study of a group of modern humans erroneously described (by Kollman, 1905, and many others subsequently) as neotenic simply because they exhibit considerable paedomorphosis. It is surprising in light of their small size and the amount of anthropological interest focused upon them that human pygmies have never been the object of a detailed allometric or heterochronic investigation. Their characteristic proportions have previously been interpreted as distinctive features that were either primitive retentions (Marquer, 1972) or adaptations to hot, humid climates (Hiernaux, 1977; see Shea, in press, for discussion). However, work now in progress (Shea, in press; Shea and Pagezy, 1988; Shea and Gomez, 1988; Shea and Bailey, 1989) suggests that almost all of the skeletal and external body proportions that differentiate human pygmies from their larger neighbors (see Table 2) are in fact the result of ontogenetic scaling or are the differential extrapolation/truncation of common patterns of growth allometry (see Table 3 and Fig. 5). The data presented in this paper are from Shea and Pagezy (1988) and represent a comparison of Twa pygmies with the Oto. Similar results are reported by Shea and Bailey (1989) for a comparison of the Mbuti Efe pgymies with other Africans. The frequency of ontogenetic scaling in human pygmies means that they do indeed have a juvenilized or paedomorphic morphology, but this is clearly not the result of fundamental dissociation and retardation of ancestral allometries. Instead, this paedomorphosis results from hypomorphosis. Whether pygmies grow for *as long* as their larger neighbors has been a question of interest for some time, but the answer has remained elusive since the pygmies are not concerned about their birth date and exact chronological age. Thus, most previous studies of pygmy growth (e.g., Merimee et al., 1982, 1987) have had to rely totally or in part on estimated ages. Recent endocrinological work on East African pygmies supports previous claims that their small size results from lowered levels of the important growth hormone insulin-like growth factor 1 (IGF-1) during the adolescent growth spurt (Merimee et al., 1987). Growth data on Efe pygmies and Lese horticulturalists of known age collected by R.C. Bailey and others from the Harvard Ituri Project indicate that significant differences in growth rates probably occur even during early growth and not just during adolescence (Bailey, 1989). These data are very relevant in the context of heterochrony, and they suggest that the small size and paedomorphic shape of human pygmies

TABLE 2. (From Shea and Pagezy, 1988) Anthropometric measurements and shape ratios for adult Oto (non-pygmy) and Twa (pygmy) groups

	Oto		Twa	
Variable	M	F	M	F
Weight (kg)	(202)	(217)	(46)	(94)
	58.8*	50.9*	48.8	44.7
	(8.1)	(9.1)	(7.7)	(6.1)
Height (cm)	(201)	(223)	(46)	(90)
	168.0*	158.8*	158.8	152.3
	(7.1)	(7.6)	(7.5)	(6.9)
Height to ASIS[1] (cm)	(194)	(208)	(45)	(90)
	95.7*	90.6*	87.7	85.2
	(5.1)	(6.7)	(5.2)	(4.7)
Chest-AP[2] (cm)	(196)	(215)	(45)	(88)
	17.2*	16.1*	16.2	15.0
	(1.4)	(1.8)	(1.8)	(1.3)
Chest-TRANS[3] (cm)	(196)	(213)	(45)	(88)
	24.6*	22.8	23.2	22.2
	(1.5)	(1.7)	(1.5)	(1.4)
Biacromial width (cm)	(193)	(207)	(39)	(86)
	36.8*	33.1*	34.4	31.5
	(2.2)	(3.2)	(3.0)	(3.3)
Biiliocristal width (cm)	(189)	(198)	(39)	(86)
	24.7*	24.2*	23.5	22.9
	(1.5)	(1.8)	(1.5)	(1.9)
Arm circumference (cm)	(150)	(160)	(22)	(49)
	27.8*	26.5*	25.1	23.4
	(2.6)	(3.8)	(2.7)	(2.3)

	Oto		Twa	
Ratio	M	F	M	F
Height/weight	(201)	(211)	(46)	(90)
	2.90*	3.20*	3.33	3.47
	(0.35)	(0.52)	(0.51)	(0.39)
Height-ASIS/weight	(194)	(202)	(45)	(90)
	1.65*	1.80*	1.85	1.94
	(0.20)	(0.28)	(0.28)	(0.22)
Height-ASIS/height	(194)	(208)	(45)	(90)
	0.57*	0.57†	0.55	0.56
	(0.03)	(0.03)	(0.02)	(0.02)
Chest-AP/chest-TRANS	(195)	(213)	(45)	(88)
	0.70	0.71*	0.70	0.68
	(0.06)	(0.08)	(0.07)	(0.07)
Biacromial width/height	(193)	(207)	(39)	(86)
	0.22	0.21	0.22	0.21
	(0.01)	(0.02)	(0.02)	(0.02)
Biiliocristal width/height	(189)	(198)	(39)	(86)
	0.15	0.15	0.15	0.15
	(0.01)	(0.01)	(0.01)	(0.01)
Biacromial width/weight	(193)	(195)	(39)	(86)
	0.63*	0.66*	0.71	0.72
	(0.08)	(0.09)	(0.09)	(0.09)
Biacromial width/biiliocristal width	(189)	(198)	(39)	(86)
	1.50†	1.39	1.46	1.38
	(0.09)	(0.15)	(0.11)	(0.16)
Biiliocristal width/weight	(189)	(190)	(39)	(86)
	0.42*	0.48*	0.49	0.52
	(0.05)	(0.07)	(0.08)	(0.07)

*, †significant difference (<.01, .05) between same-sex means of Oto vs. Twa adults. Values are N, $\bar{x}$, SD.

[1] Height to the anterior superior iliac spine.

[2] Antero-posterior chest diameter.

[3] Transverse chest diameter.

result from *rate* hypomorphosis rather than *time* hypomorphosis, or progenesis (Gould, 1977). The example of human pygmies serves well to demonstrate the general utility of a heterochronic approach to modern human morphological variation, but it clearly provides no evidence that neoteny was the key heterochronic process involved.

TABLE 3. (From Shea and Pagezy, 1988) Results of analyses of covariance testing for statistical equivalence of growth allometries between same sex (M,F) and same locale (Ekondo, Ntumba) groups of the Oto (non-pygmy) and Twa (pygmy)[1]

	Ekondo (Oto vs. Twa)				Ntumba (Oto vs. Twa)			
	M (69)		F (128)		M (160)		F (108)	
Variables	k	b	k	b	k	b	k	b
HT * WT	NS	NS	.001	NS	NS	.004	NS	NS
SPNHT * HT	NS	NS	NS	NS	NS	.004	NS	NS
CHESTAP * HT	NS	NS	NS	NS	NS	NS	NS	NS
CHESTRAN * HT	NS	NS	NS	NS	NS	NS	NS	NS
BIACROM * HT	NS	NS	.001	NS	NS	NS	NS	NS
BIILIOCR * HT	NS	NS	NS	NS	NS	NS	NS	NS
ARMCIRC * HT	NS	NS	.007	.070	NS	NS	NS	NS
SPNHT * WT	NS	NS	NS	NS	NS	.001	NS	NS
CHESTAP * WT	NS	NS	NS	.003	NS	NS	NS	NS
CHESTRAN * WT	NS	NS	NS	NS	NS	NS	NS	NS
BIACROM * WT	NS	NS	NS	NS	NS	NS	NS	NS
BIILIOCR * WT	NS	NS	.004	NS	NS	NS	NS	NS
ARMCIRC * WT	NS	NS	NS	NS	NS	NS	NS	NS
BIACROM * BIILIOCR	NS	NS	NS	NS	NS	NS	.002	NS
CHESTAP * CHESTRAN	NS	NS	NS	NS	NS	NS	NS	NS
SPNHT * BIILIOCR	NS	NS	NS	NS	NS	.001	NS	NS
ARMCIRC * CHESTAP	NS	NS	.006	.004	NS	.001	NS	NS

[1] The values k and b refer to slope and intercept for the equation log y = k log x + log b. Level of statistical significance utilized is $P < .01$.

[2] Anthropometric variables are height (HT), weight (WT), height to the anterior superior iliac spine (SPNHT), anteroposterior (CHESTAP) and transverse (CHESTRAN) chest diameters, biacromial width (BIACROM), biiliocristal (BIILIOCR) width, and arm circumference (ARMCIRC).

The Kalahari bushmen of southern Africa present an additional such example. Numerous morphological attributes of this group have been characterized by anthropologists (e.g., Drennan, 1931; Dart, 1940; Tobias, 1957) as the result of neotenic paedomorphosis. To the extent that these morphologies are truly paedomorphic, and until it is clearly demonstrated otherwise, virtually all of them should be interpreted as the result of the small body size and reduced growth rates (i.e., rate hypomorphosis) that also characterize this group.

It seems quite clear that early hominids potentially ancestral to the genus *Homo* were considerably smaller than we are (Jungers, 1988), and thus we no longer accept scenarios, such as that proposed long ago by Weidenreich (1946), of descent from giants. On the other hand, recent fossil discoveries (Johanson et al., 1987; Leakey and Walker, 1985) also clearly reject any claims for a progressive and linear *increase* in body size within *Homo* over the past 2 million years or so. If future discoveries suggest that fully modern humans exhibit decreased stature and weight compared to either *Homo erectus* or early *H. sapiens,* then we might expect some paedomorphic or juvenilized features such as gracilization, smaller joint surfaces, etc., in modern humans. But such changes in shape would represent paedomorphosis via *hypomorphosis* (i.e., simple allometric correlates) and emphatically not paedomorphosis via *neoteny.* Most of the cranial features among various early fossil hominids presented as evidence of neoteny by Privratsky (1981) fall into this category of misinterpretation.

Growth prolongation vs. shape retardation

The fact that prolongation of growth in time does not equal or require the dissociation and retardation of patterns of shape change is fundamental to understanding the debate over human neoteny. The equation of growth prolongation with shape retardation has played a pernicious role in this debate, first because it is an erroneous prediction based on what we know of heterochrony, and second because the prolongation of growth periods in human evolution is so clearly true that many have simply leaped to the interpretation that the neoteny hypothesis (as so defined) must therefore also be correct. Recall from the outline presented above

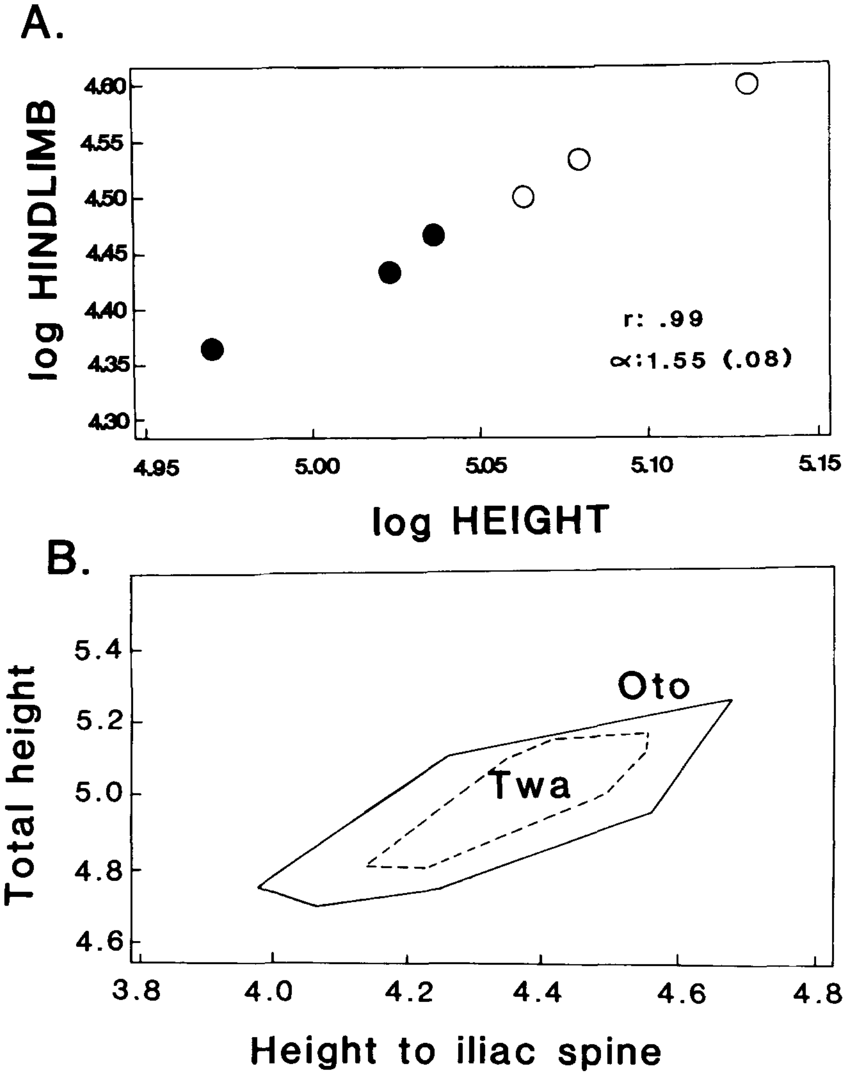

Fig. 5. **A:** Allometric comparison of lower limb length vs. height in a series of adult means of pygmy (solid circles) and non-pygmy (open circles) Africans. **B:** The polygons enclose ontogenetic data scatters for Twa pygmies and Oto villagers in a plot of total height vs. height to the anterior superior iliac spine, roughly a measure of lower limb length. Note the concordance with a single allometric trajectory of size/shape change in both cases.

that in a pure case of neoteny there is no expectation of prolonged growth in time or delayed maturity (Fig. 1C, 4C), merely the dissociation and retardation of allometric shape trajectories (reflected in either decreased slopes or downward transpositions for positively allometric trends, and increased slopes or upward transpositions for negatively allometric trends).

Gould (1977:375–376) argued for an inevitable covariation between length of the growth period and retardation of underlying shape changes:

> The key to a proper understanding of human paedomorphosis is not the simple enumeration of putatively juvenile shapes in human adults, but rather the doc-

> umentation of a general matrix of retarded development within which adaptive paedomorphosis can readily occur.

In a footnote to this passage, he stated:

> As I have emphasized continually, not all types of retardation imply paedomorphosis; hypermorphosis (with recapitulation) is also an aspect of retardation. But hypermorphosis involes a delay in reproductive maturation alone, dissociated from all other aspects of somatic development. Human retardation is a pervasive phenomenon of almost all systems, somatic and germinal. *General retardation of this sort entails extensive paedomorphosis as an almost ineluctable consequence.* (Italics mine.)

If true, this claim would be a very important and supportive key to the neoteny debate. But what sorts of genetic, developmental, or correlational evidence do we have to support this general claim, and what about the specific human case? What we know about major growth control substances (growth hormone, etc.) or patterns of overall growth in time provides little if any support (contra Privratsky, 1981) for a claim that extending the duration of growth periods would inevitably lead to paedomorphosis (see below). What would be the developmental mechanism underlying such covariation? Significantly, Gould (1977) provided no evidence or even discussion of the corresponding parallel development, i.e., early maturation or truncation of growth periods (time hypomorphosis or progenesis) presumably being inevitably linked to acceleration of morphological change.

One hypothetical situation that might fit these predictions (and also might apply to the human brain, a common focus in the neoteny debate), is the case where early and late ontogeny are characterized by dramatically different scaling patterns. Consider for heuristic purposes that postnatal growth of a region is divisible into two periods, the first positively allometric with respect to overall size and the second negatively allometric, and that these periods are independently controlled by different growth hormones. In this case, an extension of the first growth period in time will result in relative enlargement (and thus paedomorphosis), but only as long as the second growth period is not correspondingly extended, since this would result in comparable or even greater relative diminution. In humans, we do extend in time the early period of rapid prenatal and early postnatal brain growth (Weidenreich, 1941), thus attaining a relatively juvenilized gross skull form with a large, bulbous cranium. Apart from some qualifications to be discussed below, I consider the relative size of the brain and neurocranium as evidence of neoteny. But how many other structures or regions follow such a pattern and can be similarly explained? Almost none, to my knowledge, and thus there seems to be little in the way of coordinated morphological juvenilization that can be attributed to simple extension of the various growth periods.

A brief consideration of the variation among different primate species or among various human groups also reveals no necessary correspondence between extension of growth periods and retardation of shape change. Figure 6 is a comparison of life histories in humans and other primates. It is often used to demonstrate the extended growth periods and delayed maturation of humans relative to other primates. But a comparison of great apes to monkeys yields a similar strong trend of increased duration and delayed maturation, as does a comparison of monkeys with prosimians. If neoteny were a necessary consequence of such developmental shifts, should not adult chimpanzees, orangutans and gorillas look like fetal or juvenile monkeys? What about other long-growing and late-maturing mammals? Cetaceans and elephants are not particularly paedomorphic, as Slijper (1936) pointed out long ago. These findings do not strengthen the argument for pervasive morphological paedomorphosis in the face of extended duration of growth.

We can also reverse the purported correlation between neotenic paedomorphism and the extension of growth periods and delayed maturation. If our species is the

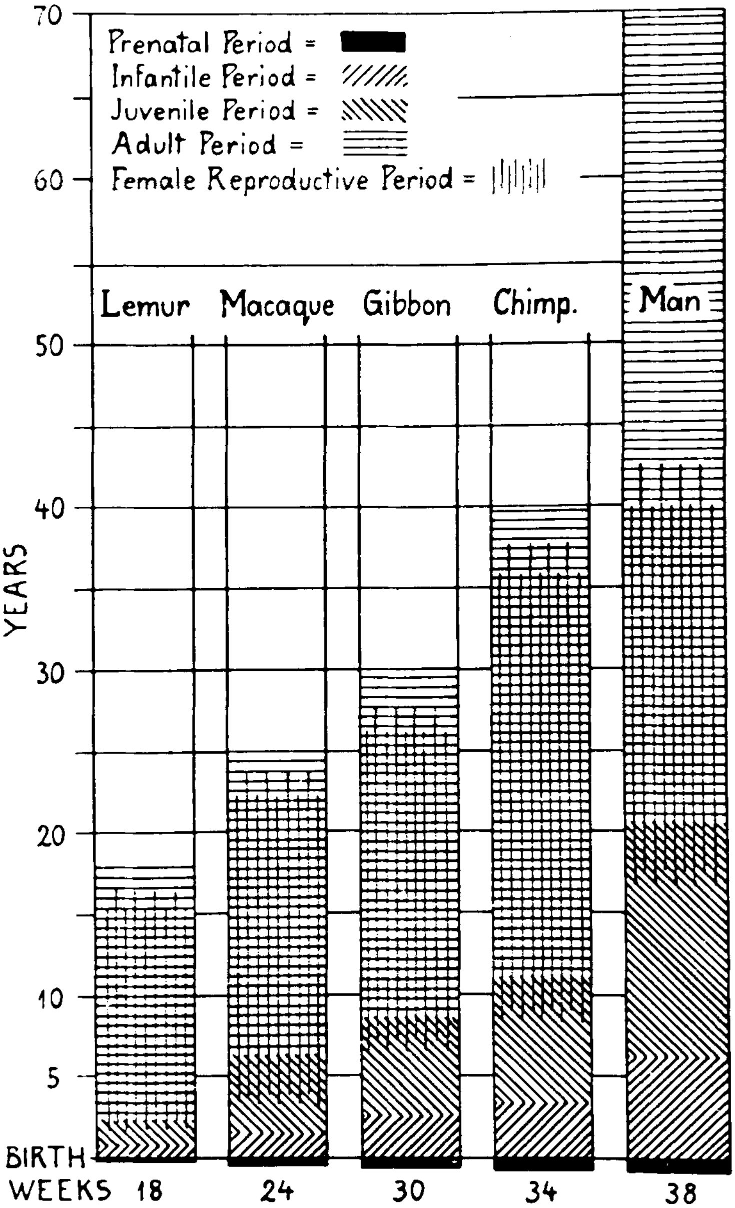

Fig. 6. (From Schultz, 1969.) A comparison of various life history stages in selected primates.

product of integrated neotenic processes, and if various human groups exhibit differential paedomorphosis as claimed by most advocates of neoteny from Bolk to Gould, then should we not find in certain of these an extension of growth periods and time to maturity? There is no evidence whatsoever to support such a claim. The African pygmies and the Kalahari San bushmen described above exhibit some paedomorphic features, but clearly no delay in maturation or prolongation of respective growth periods. Mongoloids are frequently cited as the most neotenic of human groups, yet a careful consideration of various criteria of skeletal, dental, and pubertal development reveals no evidence of delayed maturity or prolonged

TABLE 4. Age of menarche in various human groups[1]

Place	No. of studies	Mean value (yr)
Europe	26	13.3
Descendants of Europeans abroad	9	12.9
Africa	13	14.9
Descendants of Africans abroad	3	13.2
Near East and India	14	13.6
Asiatics	14	13.1
Pacific Islanders	8	16.2

[1] Data are extracted from Table 15 (pp. 214–215) of Eveleth and Tanner (1976) and represent average values determined for a series of median values as given by various studies.

growth in this group (Eveleth and Tanner, 1976). Table 4 summarizes data from Eveleth and Tanner (1976) on age of menarche is various human groups, and again there is no evidence for prolonged growth and delayed maturation in Mongoloids or Asiatics. It is also worth reemphasizing in this context that most of the paedomorphosis taken as evidence of neoteny in Mongoloid or Asian groups probably reflects allometric correlates of small size.

The equation of prolonged growth with neotenic paedomorphosis has led to other interesting inconsistencies. Geist (1971) describes male bighorn sheep as "neotenous" because they continue to grow and mature behaviorally for 5 to 6 years after they become capable of reproduction. This prolonged growth results in age- and size-related dominance criteria: "... one finds age-dependent horn-size differences among rams, which can be used by the animals to predict the dominance rank of strangers" (Geist, 1971: 349). But this type of sexual bimaturism and prolonged male growth leading to age- and size-related dominance hierarchies is extremely common among mammals (Wiley, 1974; Jarman, 1983; Shea, 1986). As I have stressed elsewhere (Shea, 1986), in such cases the male morphology relative to the female's is not indicative of paedomorphosis via neoteny, but rather peramorphosis via time and/or rate hypermorphosis. The males grow longer and bigger and exaggerate their allometric structures accordingly, but this entails no neotenic dissociations or pervasive paedomorphosis. Geist (1971) seems to acknowledge this in part when he refers to females as paedomorphic because as adults they resemble *young and small* males (as above, this does not make the females neotenic either—their paedomorphosis results from hypomorphosis relative to males, not neoteny).

Although Gould (1977) accepts Geist's (1971) claim for male neoteny in the case of the bighorn sheep, a careful comparison reveals neither a proper fit with the expectations of heterochrony nor a demonstrated covariation of prolonged growth with juvenilization. Among primates, the large and strongly dimorphic gorillas provide an example that nicely parallels Geist's bighorn sheep, since males undergo prolonged growth in size and secondary sexual characteristics that signal information on dominance and fitness to their conspecifics (Shea, 1985). But if gorillas are "neotenous," as suggested by Geist's criteria, and we humans are also neotenous, as suggested by many others, and pygmy chimpanzees are neotenous as well, as I will in fact suggest below, then just what utility can such a label possibly have, especially when common chimpanzees might arguably serve as a model for the hypothetical common ancestor of all of these? Clearly, male gorillas and male bighorn sheep are not neotenic relative to female conspecifics (instead they are hypermorphic), and only a mistaken belief that prolonged growth periods are inexorably characteristic of, or linked to, paedomorphosis via neoteny would produce such a claim.

In sum, comparative examination of other mammals provides no evidence that prolongation of growth periods necessarily leads to retardation of shape change. Humans are indisputably long-growing mammals, and the relationship of this life history pattern to extensive learning, elaborate communication, complex social interactions, and large brain size that many previous authors have discussed is undoubtedly true in large measure. But we have extended *all* of our life history periods, not merely the embryonic or juvenile ones. Lovtrup (1978) also suggests that human ontogeny is best characterized as simply prolonged (in time) rather than retarded (in rates of shape differentiation). Furthermore, I see no convincing evidence that these developmental extensions resulted in a pervasive morphological paedomorphosis in extant humans. An additional argument against neoteny has recently been made by Bogin (1988), who claims that the human pattern of growth includes two novel features not seen at any point among nonhuman primates: the addition of the childhood period and the markedly increased potential for statural growth at adolescence. These various issues may remain open to further testing. The point I wish to stress here is that the data probably cited the most frequently in support of neoteny, i.e., our long growth periods, in fact provide no such verification. The data are not wrong; it is the predictions that are fallacious.

A superficial similarity?

Another set of much-discussed features, principally within the skull, qualifies as somewhat "juvenilized" in form at first glance, but upon closer examination suggests the possibility of a merely superficial resemblance. For example, consider the skulls of gibbons and humans. There are some superficial similarities (especially when both are compared to something like a gorilla), such as a relatively short face and relatively large brain case. But more detailed study reveals many fundamental differences in facial, basicranial, and neurocranial morphology (Schultz, 1973; Shea, 1988b). In fact, there is no basis for inferring any close shape connection between the skulls of humans and gibbons, as Gould (1975) did following DuBois (1896) in his discussion of geometric similarity, or as Kluge (1983) and Bonde (1984) did in arguing that prognathism in the great apes is a synapomorphy while humans and gibbons retain a homologous plesiomorph condition (see Shea, 1988b). This example nicely illustrates the relevant point that we must look beyond extremely simple shape indicators such as relative face or brain case size to get at the question of homologous growth processes and trajectories. If a derived species comes to be superficially paedomorphic, but via substantially different pathways than those characterizing the ancestral ontogeny, a hypothesis of simple heterochronic transformation is unlikely.

Many contentious features in the neoteny debate potentially fall into this category, but only a few can be discussed here. The extensive literature on basicranial flexions has been reviewed by Gould (1977); his comments and a perusal of the literature cited provide a good introduction to this topic. In a recent paper, Moss et al. (1982) extend the earlier critical observations of Starck (1962), Hofer (1965), Kummer (1952, 1960), Dullemeijer (1975), and others regarding basicranial flexion homology and the neoteny hypothesis. Using sectioned fetal and young skulls, as well as descriptions and illustrations from the literature, they find fundamental dissimilarities in the skull base of humans as compared to other primates of any developmental stage. Specifically, they argue that the composition of the anterior cranial base, plus the sites and amount of flexion of the human brain and cranial base, are uniquely different at all developmental stages in humans (Moss et al., 1982) and do not closely resemble the fetal or young stages of nonhuman primates. Thus, the frequently cited similarity in basicranial flexion between adult humans and fetal or young nonhuman primates is a superficial resemblance that belies rather different and specific morphogenetic processes. Gould (1977) basically concedes this point, but argues that this is hardly a fatal blow to the larger hypothesis.

The detailed anatomy of the pharyngeal surface of the skull base has also been cited as evidence against the neoteny hypothesis and as support for a superficial rather than homologous similarity. In a series of papers, Laitman, Crelin, and colleagues have carefully demonstrated the sequence of developmental changes in soft tissue and skeletal anatomy of the basicranium, upper respiratory system, and vocal tract region in modern humans as compared to fossil hominids and nonhuman primates (e.g., Laitman and Crelin, 1976, 1980; Laitman et al., 1978, 1979; Laitman and Heimbuch, 1982). In brief, their results indicate that the strong

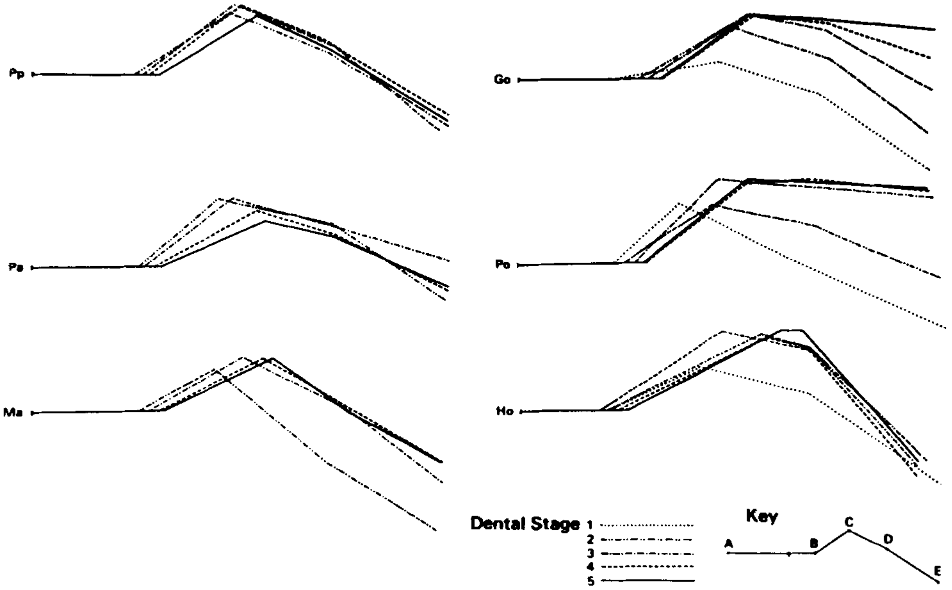

Fig. 7. (From Laitman and Heimbuch, 1984.) Development of the basicranial line in *Pan paniscus* (Pp), *Pan troglodytes* (Pa), *Macaca mulatta* (Ma), *Gorilla gorilla* (Go), *Pongo pygmaeus* (Po), and *Homo sapiens* (Ho). Basicranial points as illustrated in the key are (A) prosthion, (B) staphylion, (C) hormion, (D) sphenobasion, and (E) endobasion. Note the considerably greater shape change during development in *Homo* as compared to *Pan paniscus*. Note also the unique basicranial flexions seen in *Homo*.

flexion characteristic of adult human basicrania taken to be evidence of neotenic paedomorphosis actually develops during postnatal growth as the tongue and larynx descend in the neck (i.e., human adult morphology changes considerably from that characterizing the fetal condition of humans and nonhuman primates alike). In fact, Laitman and Heimbuch's (1984) data demonstrate *less* change in basicranial angles and linear measures from juvenile to adult stages in *Pan paniscus* than in *Homo sapiens* (Fig. 7). Upon close examination, therefore, our adult morphology in this region does not represent the retention of fetal shapes or growth processes, but a superficial similarity produced via novel ontogenetic trajectories, and of course directly related to the functional requirements of increasing supralaryngeal space to permit modification of produced sounds. For these reasons, upper respiratory system morphology has been offered as strong evidence against neoteny of skull form in human evolution (Lieberman, 1984).

Dean and Wood (1984) have recently analyzed growth of the cranial base in hominoids and have discussed their results explicitly in the context of the neoteny debate. They examined cross-sectional growth of 10 linear and angular basicranial measurements in the large-bodied hominoids and found both increases and decreases in growth rates in *Homo* relative to other hominoids, as well as differences in size and shape present at or near birth. They concluded that differences between *H. sapiens* and the great apes were too substantial to be underlain by simple modifications in the timing and pattern of common growth patterns. They hypothesize that more fundamental and divergent changes in localized growth patterns produce the morphological distinctions in humans. Based on these results, as well as comparisons with fossil hominid basicrania (Dean and Wood, 1982), the authors concluded the following (Dean and Wood, 1984:178):

> It would then be an over-simplification, even within the broader definition of Gould (1977), to regard the human cranial base a[s] "neotenous," or to consider

the modern human cranial base pattern as a paedomorphic form of the infant great ape, or infant primitive hominoid, cranial base pattern.

Another form of recent evidence relevant to issues of facial growth is the use of scanning electron microscopy to reconstruct patterns of bone growth and remodeling. Bromage (1985, in press) has compared facial and mandibular growth in modern humans, chimpanzees, the Taung child (*Australopithecus africanus*), and a series of other gracile and robust australopiths. He concludes (in press) that while facial growth patterns in both australopiths and early *Homo* fundamentally resemble the primitive facial remodeling pattern characteristic of chimpanzees, the pattern in modern *Homo* results from uniquely derived ontogenetic remodeling trajectories (e.g., resorption over much of the midface). Bromage (in press) concludes:

> . . . divergent heterochronic growth processes have been shown to characterize the phylogenesis of this growth pattern during the course of human evolution . . . whereas heterochrony most certainly reflected evolutionary change associated with the emergence of the human lineage (Gould, 1977), the heterogeneity of heterochronic processes suggests that the global concept of neoteny could not have accounted for the ontogenetic sequences characterizing the evolution of the modern human craniofacial complex.

These results from SEM analysis support the conclusions of Enlow (1968) based on histological studies. Fairly extensive data for a variety of other higher primates (see Moore, 1982, for a summary) clearly seem to indicate that the human remodeling pattern of extensive resorption over the anterior aspect of the facial skeleton is unique. It is not the result of the simple retention of juvenile remodeling patterns and rates.

As a final example in this section, let us consider the relative size of the human brain, long the anthropocentric focus of the neoteny debate. Although Weidenreich (1941) made a number of good points in arguing against Bolk's (1926, 1929) interpretation of human brain size as the result of neoteny, I basically concur with Gould's (1977) argument that the key issue is the extension in size and time of the rapid early growth of the brain. In a real sense this is a fetal retention via dissociation of the normal postnatal negative allometry, and thus good evidence for neoteny in terms of expected allometric patterns (see Table 1 and Fig. 4). However, total gross size of the brain is admittedly a rather superficial focus, especially since we know that the regions of this complex structure exhibit their own variable growth trajectories and allometries. Passingham (1975) has shown that certain proportions within the human brain are just what would be expected given total brain (not body) or neocortex size, supporting the neotenic argument. However, while the *relative size* of the human brain (and the vault housing it) resembles juvenile stages of our ancestors, and within-brain proportions are *largely* what would be expected given total brain size, humans have uniquely developed certain specialized regions, such as the enlarged cortical areas concerned with speech, as well as disproportionately enlarged association and motor cortex (Passingham, 1975), and possibly reorganized aspects of thalamic nuclei proportions (Passignham et al., 1986). These within-brain proportions are not characteristic of the fetal or juvenile stages of our close relatives (Ewer, 1960) or predicted expectations given within-brain allometries (Passingham, 1975) but rather are neomorphic proportions presumably underlain by derived developmental patterns and the result of selection for particular abilities and behaviors during hominid phylogenesis. Holloway (1979) provides a review of possible non-allometric reorganization of brain components in human evolution. Additional data for humans and nonhuman primates are required to further clarify this interesting problem, although once again a careful examination casts doubt on the accuracy of interpretations of simple neotenic paedomorphosis. Such an ontogenetic and phylogenetic interpretation of the brain should hardly be surprising for the brainiest and most behaviorally derived of mammals.

In sum, detailed analyses of craniofacial development and morphology appear to provide little support for pervasive neotenic mechanisms in the evolution of modern human skull form. Our relatively large neurocranium and relatively small face superficially resemble the juvenile stages of our close relatives (Creel, 1986), but this similarity does not appear to be particularly informative in developmental or evolutionary terms. In a different context, Pilbeam and Gould (1974:899–900) made an analogous point:

> *Australopithecus africanus* has a rounded braincase because it is a relatively small animal; *H. sapiens* displays this feature because we have evolved a large brain and circumvented the expectations of negative allometry. The resemblance is fortuitous; it offers no evidence of genetic similarity.

Similarly, the resemblance between adult humans and juvenile primates in gross neurocranial/splanchnocranial proportions offers little evidence of a simple and coordinated dissociation of homologous developmental processes.

Non-paedomorphic shape changes

That many aspects of human growth and morphology cannot be considered to be the result of neotenic paedomorphosis is well known, and such features have previously been noted and discussed by both advocates and detractors of the neoteny hypothesis. Schultz (1969, and references therein) in particular stressed the fact that human morphological features were underlain by a great variety of accelerations, retardations, extensions, and other developmental bases, with no single type of modification being pervasive. Just a few of the accelerations noted by Schultz (1969), which characterize human growth and evolution and which directly contradict the predictions of neoteny, are early fusion of the central and navicular bones of the wrist, early fusion of the sternebrae, and early descent of the testes. In addition, two other non-paedomorphic features of human morphology are pelvic shape and the marked flexion of the vertebral column at the lumbosacral border (Schultz, 1950). References cited herein and in Gould (1977) can be consulted for many additional non-paedomorphic developments in human evolution.

These and other contradictions to the predictions of neoteny are granted by Gould (1977) and various advocates, with the reasonable claim that exceptions to neotenic paedomorphism must exist given a modern appreciation of mosaic evolution. This is true in principle, as discussed at some length in the following section. However, the central point is that the significance of the neoteny hypothesis (or any purported key to hominization) lies in its ability to account for those features of our clade and lineage that are novel developments, since these are literally what set us apart from our close relatives. As has long been appreciated, the two most important of such features are large brain size (with its restructured architecture and all of the behavioral causes and consequences that go with that) and bipedal locomotion. The possible neotenic context of hominid brain evolution was discussed earlier in this paper. In addition, few, if any, of the pervasive morphological changes associated with our extremely specialized form of bipedal locomotion can be interpreted as the result of neotenic paedomorphism (Gould, 1977). This severely limits the model's applicability to human evolution.

Of enumeration and testability

One of Gould's primary complaints against those critical of the neoteny hypothesis is that they argue in what he refers to as the "enumerative tradition" (1977: 363):

> . . . the *experimentum crucis* has been cast in the following way: enumerate as many morphological features as you can and judge which are paedomorphic and

> which are not. If you regard a vast majority, or perhaps merely a "basic" list, as paedomorphic, you accept the hypothesis; if you disagree with this claim, you reject the hypothesis.

Gould (1977:362–364) further argues that "this tradition, in subtle ways, still hinders the application of new and more fruitful approaches"; that it "is the worst way to carry on the discussion"; and that theories in natural history are not "proved or disproved by amassing a compendium of empirical results, listing those items that fit the theory and those that do not, and comparing the lists."

We can certainly agree with Gould's lament that the criterion of acceptance in practice often reduces to lining up features in two columns, with little knowledge of or concern for important biological considerations such as homology, genetic and epigenetic bases, covariation, allometric factors, and so forth. Such a situation is often also seen in studies of phylogenetic reconstruction, where scores of characters, most not weighted or well understood in terms of developmental and/or functional correlations, are added and subtracted to arrive at the most parsimonious arrangment. But if it is sometimes too simplistic to manufacture long lists of features pro and con, it is also misleading to think that we could maintain a central role for the process of neoteny in hominization if a vast majority of the features we could assess were clearly not paedomorphic and/or the product of neotenic dissociations. As I noted previously, the primary value of a heterochronic approach to morphological differences lies in the discovery of suites of covarying characters that might not otherwise be perceived as interrelated. So, at some level, we must assess the congruence of *observed* morphological patterns and underlying processes with those *predicted* by the hypothesis. How else to do this but tabulate the results of such tests?

It is interesting that after his criticism of argument in the enumerative tradition on pages 363–364, Gould (1977) lays out his primary evidence for neoteny, and then proceeds to rebut one by one the major workers who have tried to refute the neoteny hypothesis. Finally, in the face of these purported exceptions, he provides his most specific criterion for acceptance or rejection of the hypothesis (1977: 380), and in so doing, enlists the form of argument that he previously criticized:

> The issue is not whether exceptions to a general paedomorphosis exist (they must); it is, rather, their *extent.* If they should overwhelm the paedomorphic features in *frequency* and *importance,* then we could maintain no general hypothesis of neoteny. (Italics mine.)

A consideration of the extent and frequency of discordance between observed and predicted results is certainly an appeal to testing in the enumerative tradition. Since the neoteny debate must be treated as any other scientific (i.e., testable) hypothesis, this is entirely appropriate.

Despite this lapse into enumerative empirical argument, there is much to be said for Gould's (1977:364) claim that "theories are tested by examining the processes that yield the results and by judging whether these processes are consistent with more general theories." I believe the evidence analyzed in this paper provides an ample test for the neoteny hypothesis according to these criteria, as opposed to simple enumeration of trait lists.

An additional aspect of testability is central to Gould's (1977) analysis of this debate. He writes:

> I believe that human beings are "essentially" neotenous, not because I can enumerate a list of important paedomorphic features, but because a *general, temporal retardation of development has clearly characterized human evolution. This retardation established a matrix within which all trends in the evolution of human morphology must be assessed.* (Italics in original, Gould 1977: 365).

The problem here is that this approach seemingly removes all morphological tests of the predictions regarding neotenic dissociation and retardation (recall that retardation here refers to decreased rates of *morphological* shape change, while in the passage above Gould is using retardation to mean prolongation in time of growth periods—this difficulty and inconsistency was discussed earlier). In a literal sense, it makes human neoteny true by definition and declaration, even though it has been shown in comparative studies that temporal retardation of development by no means inevitably results in neotenic paedomorphosis in nonhuman primates or other mammals. This apparently a priori commitment to the veracity of the netoeny hypothesis appears to be at work when Gould (1977) discussed some of the obvious exceptions that were noted previously. Certain of these are interpreted as actually supporting the hypothesis in a roundabout way, since they are the result of hypermorphic peramorphosis (see Fig. 1E), and this involves a prolongation of growth periods. Others are viewed as true accelerations, but these and other such exceptions (presumably whatever their extent) cannot possibly bring about the model's collapse since temporal retardation is taken as the only meaningful criterion for acceptance. Virtually every morphological development in human evolution has occurred within this so-called matrix of retardation. Are all to be taken as evidence of neoteny, therefore?

A Neotenic Hominoid

In the preceding sections, the developmental patterns, adult morphologies, and life history features observed in modern humans have been weighed against those predicted by the traditional categories and processes of heterochrony. An additional approach that also provides an important perspective on this debate is to consider whether any of the other hominoids may serve as examples of neoteny. I have argued previously (Shea, 1983b, 1984, 1988a) that many of the morphological (and perhaps some behavioral) differences between the pygmy or bonobo chimpanzee, *Pan paniscus,* and its close relative the common chimpanzee, *Pan troglodytes,* should be viewed as an integrated suite of characters resulting from neoteny. This example provides a much better fit with the various expectations for neoteny in the traditional heterochronic framework, as for instance does the case of Gould's (1977) land snails. First of all, neoteny in the chimpanzee case affects a large region of the body, the skull, via a fundamental dissociation and retardation of allometric trajectories of shape change. This is illustrated in Figure 8. Trajectories of shape change within the face exhibit markedly lower slopes in *P. paniscus* when compared to measures of overall body size and growth. This results in strongly paedomorphic skull form, as noted by Coolidge (1933) and reconfirmed in detail by many subsequent workers (e.g., Weidenreich, 1941; Fenart and Deblock, 1973; Cramer, 1977; Shea, 1983b,c, 1984; Laitman and Heimbuch, 1984). McHenry and Corruccini (1981) nicely illustrated this cranial juvenilization by comparing size reduction of the face with that of the humerus (see Fig. 8). Shea (1982, 1984a) used cranial coordinate maps to show that adult *P. paniscus* skulls cluster with those of juvenile *P. troglodytes* having only their second permanent molar erupting, while hindlimbs are the same size in adults of the two species (Shea, 1981; Zihlman, 1984) and the trunk and forelimbs are only slightly reduced in size in adult *P. paniscus* (Shea, 1984). Means of cranial and postcranial dimensions for chimpanzees of different dental ages summarized in Table 5 illustrate the small skull size of *P. paniscus.* Thus, we see a gradient of size reduction and paedomorphosis with its strongest expression in the facial region (Shea, 1983a, 1984—see Fig. 8).

Additional detailed considerations of this chimpanzee example only strengthen the claim for cranial neoteny in *P. paniscus.* The considerable amount of work done on skull growth and form in both of these closely related species yields no reason to suspect that divergent or non-homologous growth processes underlie the similarity between adult *P. paniscus* and juvenile *P. troglodytes.* As previously noted, using the degree of departure from fetal and juvenile morphologies as a criterion for neotenic paedomorphosis (Gould, 1977), both linear and angular dimensions

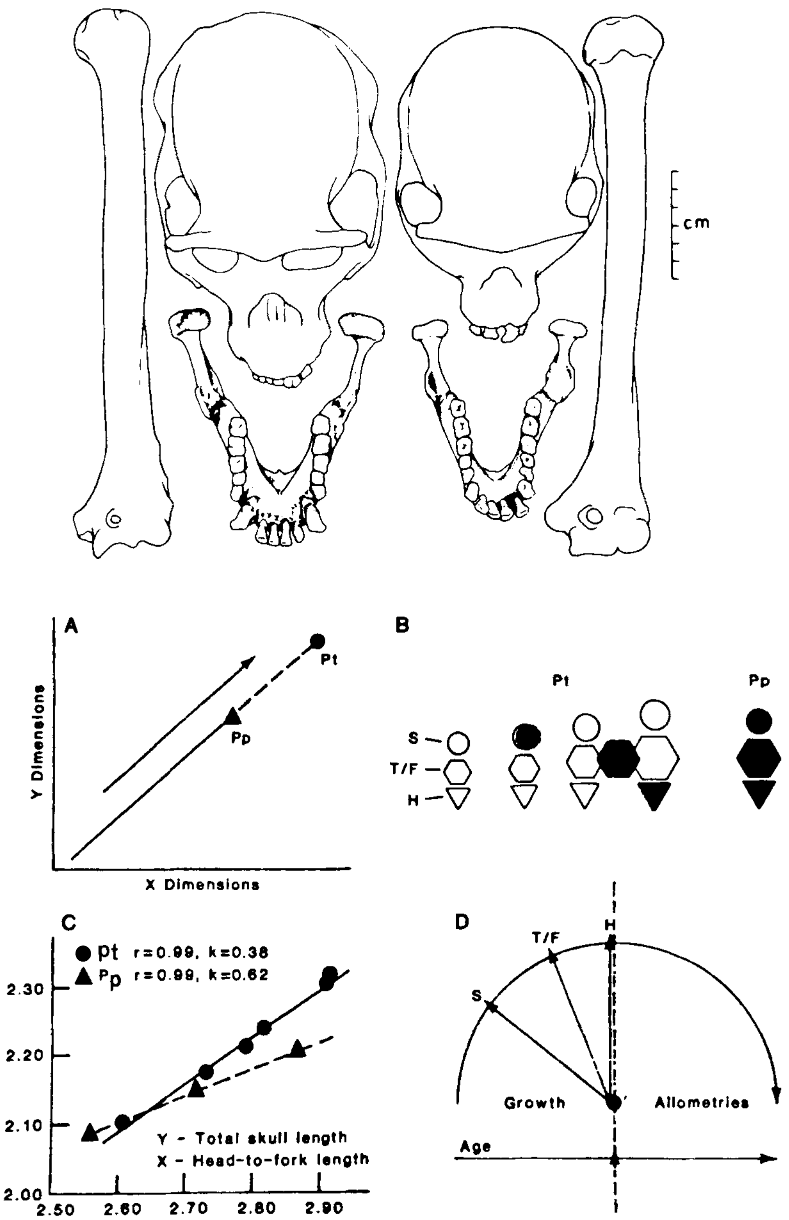

Fig. 8. (After McHenry and Corruccini, 1981; Shea, 1983b.) Cranial paedomorphosis via neoteny in bonobos, or pygmy chimpanzees (Pp), as compared with common chimpanzees (Pt). The upper portion of the figure is a comparison of the humerus and skull, illustrating the marked diminution of skull size as compared to postcranial size in *P. paniscus*. The lower panel of the figure schematically illustrates that within major anatomical regions, the two species of chimpanzees exhibit ontogenetic scaling, or the differential extension of common patterns of growth allometry (**A**), and that skull size is more markedly paedomorphic than postcranial regions (**B**). In **C**, a plot of skull length against a measure of overall size (trunk length) reveals an allometric dissociation and retardation of shape change in *P. paniscus* (note the lower slope; note also that the symbols are reversed, and the solid triangles are Pp, the solid circles are Pt.) In **D**, the marked paedomorphosis of the skull (S) relative to the trunk and forelimbs (T/F) and the hindlimbs (H) are schematically depicted by independent vectors using a clock model (dashed midline equals the value for Pt).

TABLE 5. Mean values for Pan paniscus *(Pp) and* Pan troglodytes *(Pt) of different dental ages*[1] *and for three cranial and two postcranial dimensions*[2]

	Palate length[3]				Face length				Skull length				Arm length				Leg length			
Dental	Pp		Pt		Pp		Pt		Pp		Pt		Pp		Pt		Pp		Pt	
Ages[1]	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Y	34	33	38	37	41	40	43	43	66	66	75	73	—	—	—	—	—	—	—	—
3	40	40	51	47	50	49	59	56	77	75	94	90	—	—	382	365	—	—	354	340
4	47	52	56	59	55	62	62	64	89	97	106	108	—	—	414	421	—	—	393	401
5	56	53	66	61	66	63	69	69	105	101	123	117	491	—	523	485	482	—	499	457
6	56	59	74	70	65	68	85	77	105	111	139	132	546	556	578	573	535	533	546	541
7	61	59	80	75	70	69	89	83	114	101	145	136	559	559	577	567	549	549	549	537

[1] Y = deciduous dentition; 3 = M1 erupting; 4 = M2 erupting; 5 = M3 erupting; 6,7 = adults

[2] Arm length = humerus + radius lengths; leg length = femur + tibia lengths. M = male; F = female.

[3] All lengths in millimeters.

suggest that adult *P. paniscus* change less than adult *H. sapiens* (Laitman and Heimbuch, 1984). In terms of body size and developmental timing features, *P. paniscus* fits the expectations of traditional heterochronic categories and processes. There is no indication that *P. paniscus* matures and ceases growth any earlier (or later) than *P. troglodytes* (Shea, 1984), thus ruling out time hypomorphosis as the appropriate heterochronic process yielding the paedomorphic morphology of the skull. Furthermore, although there is considerable debate regarding body weights and overall body size in *P. paniscus* as compared to *P. troglodytes* and its various subspecies (Jungers and Susman, 1984; Shea, 1984), it appears at present that 1) whatever overall size differences exist between pygmy and average common chimpanzees, they are not large and clearly vary with the body region being compared; and 2) *P. paniscus* may weigh as much as at least one of the subspecies of common chimpanzee, *P. troglodytes schweinfurthii* (Jungers and Susman, 1984). In any case, the marked dissociation of skull (facial) growth relative to *any* measure of overall size fits the criterion for local neotenic retardation, and not the expectation of ontogenetic scaling as in the case of rate hypomorphosis (refer to Fig. 1A above). This dissociation of allometric growth of particular regions compared to one another occurs in spite of the fact that *within* each of these regions a comparison of the two chimpanzee species yields almost total ontogenetic scaling (see Shea, 1981, for within-limb comparisons; Jungers and Susman, 1984, for pelvic girdle dimensions; Shea, 1983c, for the skull and face; and Shea, 1986, for the scapula—see Shea, 1983a, 1984, for summary and synthesis). Table 6 summarizes the results of adult proportion means and ontogenetic allometric comparisons for various scapula dimensions in *P. paniscus* and *P. troglodytes*. Within-scapula shape differences are the result of simple growth allometric changes. The preponderance of ontogenetic scaling within the various body regions examined greatly increases the likelihood of homologous developmental patterns and processes.

In addition to the cranial (and some postcranial) skeleton, other regions of the body exhibit considerable paedomorphosis, although distinguishing between neoteny and rate (or time) hypomorphosis as the process underlying such juvenilization requires much more detailed knowledge of body weights than we currently have. Dahl (1985) has shown that the morphology of the external genitalia in adult female *P. paniscus* closely resembles that of juvenile rather than adult *P. troglodytes*. In addition, he argues (Dahl, 1986) that certain aspects (although not all) of the swelling and menstrual cycles of *P. paniscus* resemble those of juvenile *P. troglodytes*, particularly the length of the swelling phase and the intermenstrual interval. Nevertheless, Dahl (1986: 381) cautions that:

> . . . the swelling cycles of *P. paniscus* do exhibit some limited similarity with those of adolescent *P. troglodytes*, but in order to determine precisely the resemblance between the two, additional research must be conducted, particularly on the patterns of endocrinological fluctuation that characterize the ovarian cycles

TABLE 6. Scapula dimensions and proportion contrasts for adult Pan paniscus *and* Pan troglodytes *(upper half), combined with comparisons of bivariate growth allometries (lower half)*

Linear dimensions proportions[1]	*P. paniscus* (n = 13)	*P. troglodytes* (n = 31)	Significance
Morphological length	7.0 (4.5)	102.7 (5.7)	.002
Total breadth	139.7 (7.7)	157.2 (10.2)	.000
Supraspinous breadth	77.6 (7.1)	78.3 (8.2)	NS
Infraspinous breadth	69.3 (9.0)	86.1 (8.8)	.000
Spine length	131.6 (6.6)	139.5 (6.3)	.001
Morphological length ×100/ total breadth	69.6 (4.5)	65.5 (4.9)	.015
Supraspinous breadth ×100/ infraspinous breadth	114.7 (26.4)	92.0 (13.9)	.001
Infraspinous breadth ×100/ morphological length	71.1 (10.3)	84.1 (10.6)	.001

Regression Comparisons[2]		*P. paniscus* (n = 29)	*P. troglodytes* (n = 77)	Significance
Morphological length (y)	k	0.91 (0.04)	0.88 (0.02)	NS
vs. total breadth (x)	r	0.97	0.98	
Morphological length (y)	k	0.90 (0.04)	0.96 (0.02)	NS
vs. supraspinous breadth (x)	r	0.97	0.98	
Morphological length (y)	k	0.78 (0.07)	0.78 (0.03)	NS
vs. infraspinous breadth (x)	r	0.90	0.95	
Infraspinous breadth (y)	k	0.89 (0.11)	1.10 (0.05)	NS
vs. supraspinous breadth (x)	r	0.84	0.93	
Morphological length (y)	k	0.88 (0.04)	0.90 (0.01)	NS
vs. spine length (x)	r	0.98	0.99	
Total breadth (y)	k	0.93 (0.05)	0.99 (0.02)	NS
vs. spine length (x)	r	0.97	0.98	

[1] Mean (standard deviation) values in mm. plus results of analyses of variance for significant differences between means.
[2] Bivariate slope (k) value for log y = k log x + log b, standard error in parentheses; r = Pearson product-moment correlation coefficient; significance of differences in slope values determined from analyses of covariance.

of both adolescent common chimpanzees and adult pygmy chimpanzees, and on how these correlate with ovulation and the swelling cycles exhibited.

In addition to this type of developmental information, we would also need to know how endocrinological control of somatic growth and differentiation is coordinated with that of the reproductive system. Whatever the final outcome of additional research on these chimpanzees, however, it seems likely that they provide a much better example of neotenic paedomorphosis among large-bodied hominoids than do humans. The example of cranial neoteny in the pygmy chimpanzee also points up the fact that even if human skull and body form could be accounted for via regional heterochronic transformations, it would be misleading and counterproductive to classify both of these hominoid transformations in the same category.

As noted below for the human case, discussions of behavioral features in terms of neoteny and paedomorphosis are often problematic. Nevertheless, it is worth pointing out that several authors (e.g., Kuroda, 1979, 1980; Dahl, 1986) have described some of the behavioral features of *P. paniscus* as paedomorphic and resembling juvenile patterns of *P. troglodytes*. Examples here include play behavior, food sharing frequency, decreased social differentiation by sex, ventro-ventral copulation, and the characteristic genito-genital (GG) rubbing of females. Several of these behavioral features, such as the copulatory positioning and GG rubbing, may be directly linked to the morphological features of the juvenilized external genitalia discussed above (see Dahl, 1985, 1986).

I have argued elsewhere (Shea, 1983b, 1984) that the most important link among the morphological and behavioral distinctions between *P. paniscus* and *P. troglodytes* is the reduced social differentiation by sex. The most notable morphological change associated with neotenic facial growth in *P. paniscus* is the marked reduction in sexual dimorphism of the gnathic and total facial region. Although the canine teeth of *P. paniscus* are significantly sexually dimorphic, they are much less so than is the case in *P. troglodytes,* and the same holds true for a comparison of dimorphism in facial dimensions between the species (Fenart and Deblock, 1972, 1973, 1974). While we have much to learn regarding the intriguing behavioral distinctions between these two chimpanzee species (see Wrangham, 1986, for one recent discussion), it seems likely that the reduced sexual dimorphism in the facial region of *P. paniscus* is related to social factors such as lowered male-male and male-female aggression, increased female bonding, increased food sharing, and perhaps aspects of sexual behavior.

To this point I have utilized the chimpanzee example as a case study of neoteny, which implies a specific direction of evolutionary change, i.e. with the morphology of *P. paniscus* interpreted as derived. I have done this for the sake of illustration but wish to stress that it is far from clear that *P. paniscus* is more derived in its morphology and behavior than *P. troglodytes.* Arguments for this position may have been overstated (see Johnson, 1981; Wrangham, 1986), and I believe they may result from reactions to previous claims (even more overstated) that pygmy chimpanzees could be taken as a living prototype of the common ancestor of large-bodied African hominoids (e.g., Zihlman et al., 1978), or perhaps even from the fact that *P. paniscus* was discovered subsequent to *P. troglodytes.*

Neoteny and human behavioral traits

These discussions of pygmy chimpanzees suggest the need for a brief consideration of attempts to link morphological and behavioral traits in discussions of human neoteny and heterochrony. Gould (1977), along with many previous authors, discussed life history features such as prolonged learning periods and infant dependency in the context of growth patterns and morphological changes. I have outlined above why I think most of these developments in human evolution, while clearly accurate and important, simply do not provide evidence for neoteny as a specific heterochronic process. However, it is Montagu (1981) who has most extensively discussed "behavioral paedomorphosis" and suggested such features as primary evidence in favor of a neotenic origin for humans. Such discussions have attracted considerable favorable attention from various authors within the social sciences, perhaps contributing to a more general tacit acceptance of the claim that the (primarily biological and morphological) concept of neoteny has played a fundamental role in human evolution. I consider myself fairly far afield in trying to assess these behavioral arguments in detail, but I think a partial list of the behavioral traits of modern adult humans that are supposedly due to our neotenic origins will suffice to make a point. Montagu (1981) lists the following as evidence of neoteny in humans: the need for love; friendship; sensitivity; the need to think soundly; the need to know; the need to learn; the need to work; the need to organize; curiosity; the sense of wonder; playfulness; imagination; creativity; open-mindedness; flexibility; experimental-mindedness; explorativeness; resiliency; the sense of humor; joyfulness; laughter and tears; optimism; honesty and trust; compassionate intelligence; dance; song. Even while trying to remain flexible, open-minded, and optimistic, I can honestly only wonder how a list of such disparate traits, many of them arguably not even particularly characteristic of adult or juvenile humans (!), could ever be linked genetically and epigenetically, or, moreover, how such a package could relate in definable ways to morphological processes and features. What comes to mind here is the adage that a model that explains everything in fact explains nothing.

Genetic and epigenetic control of growth, allometry, and timing

A recurrent theme in several of the previous sections is that arguments in favor of the neoteny hypothesis of human evolution have generally been weakened as research progress has shifted the focus from static and simplistic growth results (e.g., craniofacial shape ratios) to more dynamic and complex developmental processes. This breakdown may be unfortunate for advocates of pervasive human neoteny; but, more important is the recognition that it is atypical for recent studies of heterochrony, where the elucidation of genetic and developmental controls of growth processes have generally clarified and supported heterochronic hypotheses and scenarios (e.g., Hall, 1984; Alberch and Alberch, 1981; Bonner, 1982; Goodwin et al., 1983; Atchley, 1987; Slatkin, 1987; Shea et al., 1987, in press; McKinney, 1988). In the example of human neoteny, we can state the issue simply as a question—what genetic and epigenetic evidence has accrued in support of notions of pervasive dissociations and retardation of allometric trajectories, and/or the linkage of these shape changes with prolongation of growth periods?

The best evidence for pervasive neotenic transformations with relatively simple developmental (hormonal) bases involves life histories characterized by metamorphosis. Gould (1977) effectively reviews these; the most significant cases represent the control of metamorphosis in insects by circulating levels of "juvenile hormone" and in amphibians by levels of thyroid hormones. In these examples, there is a well-understood and experimentally manipulable developmental basis for neoteny, but our knowledge of mammalian endocrinology provides no evidence for, or even likelihood of, such clear and marked neotenic transformations in our lineage. Our morphological shape changes during ontogeny are much more gradual and continuous than those characterizing metamorphosis, and for the most part we exhibit no differentiation of "juvenile" hormones from other hormones specifically affecting particular structures and time periods (see Ewer, 1960, for discussion of the differences between the amphibian and human examples). In our case, the primary metric of heterochrony must be allometry, and therefore any knowledge of the genetic or epigenetic control of allometric extensions, truncations, or dissociations is of particular relevance here. For example, Gould (1971) argued that there was a simple genetic and developmental basis for widespread allometric dissociations (i.e., vertical shifts or transpositions), which resulted in the production of geometrically scaled giant or dwarf forms. In his 1977 book, Gould continued this theme by stressing the likely existence of separate controls for *growth* (geometric size increase) and *development* (allometric shape change). Privratsky (1981) has argued that simple changes in the production of growth hormone might provide a basis for paedomorphosis via neoteny, although Gould (1971) suggested a similar basis for geometrically similar transformations. Discussion of the possible hormonal mechanisms of phenotypic change of course figured prominently in many early considerations of human neoteny (e.g., Keith, 1949; Marett, 1936; Zuckerman, 1936).

In the decade since the publication of *Ontogeny and Phylogeny* (Gould, 1977), there have been considerable advances in our understanding of the controls of growth processes (Bryant and Simpson, 1984). There are many control substances that affect aspects of bodily growth, but the most important immediate influence on general postnatal growth appears to be the hormone insulin-like growth factor 1 (IGF-1, or somatomedin C). Growth hormone (GH, also known as somatotropin) regulates the local production of IGF-1 in various regions of the body, and prepares target organs (e.g., prechondrocytes in the epiphyseal plates of the limbs) to respond to circulating IGF-1 and undergo multiplication, thus resulting in growth. In turn, amounts of circulating GH secreted by the pituitary are under neuroendocrine control. Any number of recent reviews and texts can be consulted for further information on the hormonal control of growth (e.g., Ludecke and Tolis, 1985; Raiti and Tolman, 1986).

My ongoing research suggests that altered levels of IGF-1 and GH generally produce pervasive extrapolations or truncations of skeletal and bodily growth allometries. Shifts in the amount of these growth hormones produce changes in body weight growth with no fundamental changes (e.g., slope divergences, transpositions) in the intrinsic controls of regional allometric patterns. This conclusion is based on work with several strains or populations exhibiting simple hormonal shifts: giant transgenic (MT/rGH) mice, characterized by abnormally high levels of circulating growth hormones and accelerated growth (Shea et al., 1987, in press); Snell dwarf mutant (*dw/dw*) mice, characterized by low levels of growth hormones and depressed growth (Shea, unpublished); and human pygmies, who were discussed above and have depressed levels of IGF-1 and retarded growth in overall size (Shea and Gomez, 1988; Shea and Pagezy, 1988; Shea and Bailey, 1989; Shea, 1988a, in press). Although much additional work needs to be done, we are beginning to understand the developmental control of growth allometries and their simple widespread extension and truncation, a consideration of fundamental significance for hypotheses of some types of heterochrony (processes A, B, D, and E in Figs. 1 and 4 above).

There is at present no such evidence of relatively simple developmental bases for the type of pervasive allometric dissociations and retardation required by past hypotheses of human neoteny. Furthermore, such widespread neotenic retardations appear unlikely in theory since trajectories of positive allometry require slope decreases and/or downward transpositions to yield paedomorphosis, while trajectories of negative allometry require slope increases and/or upward transpositions (compare this to the above discussion where shifts in GH and IGF-1 produce ontogenetic scaling, regardless of whether slopes are positively allometric, negatively allometric, or isometric). This fact has not been appreciated in previous discussions of allometry and heterochrony (e.g., Alberch et al., 1979).

There is also no evidence for any simple genetic and hormonal basis for the pervasive allometric dissociations that would normally be required to produce geometrically scaled morphs, contra Gould (1971). The mechanisms he discussed, specifically shifts in GH levels, generally produce ontogenetically scaled forms. These may often be described, particularly in the clinical literature, as proportioned or isometric replicas, but closer examination usually reveals either significant proportion differences produced by ontogenetic scaling of growth allometries, or geometric similarity produced by ontogenetic scaling of isometric growth trajectories (which are more common than has often been realized), and not dissociations. As examples, consider the case of African pygmies already discussed, yet given by Gould (1971) as a primary case of GH-based geometric similarity, or the giant transgenic mice, originally described as normally proportioned after a cursory examination (Palmiter et al., 1983), but shown by Shea et al. (1987, in press) to exhibit many proportion differences via ontogenetic extrapolation (the basis for the original mistake is understandable—ontogenetic trajectories of the mice are significantly, but not markedly, allometric). Thus, I believe that both comparative and developmental data combine to make scaling via geometric similarity as discussed by Gould (1971) an unlikely mechanism of evolutionary change.

These comments do not preclude the possibility of *any* neotenic or geometric dissociations, merely widespread ones produced by hormonal shifts or other such simple and pervasive systemic mechanisms. Of course regional growth changes can produce paedomorphosis by neoteny (as in facial form in *P. paniscus* above, or developmental abnormalities of limb or skull growth), but here the developmental bases are likely to involve more fundamental or intrinsic local growth controls (such as size of stem cell populations, local rates of cell division, etc.—see Bryant and Simpson, 1984), and thus be more restricted in scope. There is also no compelling genetic or developmental evidence to suggest that the factors controlling the duration of growth periods concomitantly affect growth allometries, such that neotenic dissociations of shape trajectories would be predicted as inevitable consequences of such life history changes. The comparative data contradicting such an association have been reviewed above.

In spite of this negative prognosis, the question of the genetic and epigenetic basis of neotenic transformations remains open, since we understand so little about the relevant mechanisms and growth dynamics. I believe that such research will be one of the most exciting and productive aspects of the study of heterochrony in general in the immediate future, and we can only hope that the specific process of neoteny will be elucidated as part of this endeavor. There is some indication that the growth hormone IGF-2, another somatomedin very similar to IGF-1 in structure and function, may predominantly regulate fetal, and particularly brain, growth (Atchley et al., 1984). Although there is no evidence of such at present, it is at least conceivable that prolongation of growth periods controlled by IGF-2 could lead to a suite of correlated retardations, resulting in some neotenic paedomorphosis (although only for features unresponsive to IGF-1 and other postnatal growth hormones and exhibiting complex and unusual growth trajectories like that of the brain). It is in these areas that new data could be collected to reconsider the neoteny debate in a scientifically fruitful way.

CONCLUSIONS

Heterochrony in general has undoubtedly played a central role in the evolutionary transformations characterizing our lineage, and neotenic paedomorphism in particular can probably be implicated in several of these shifts. However, a hypothesis of general and pervasive human neoteny is clearly no longer viable. A careful analysis of human development, morphology, and life history patterns reveals little concordance with the predictions of neoteny based on accepted criteria. Examples of confusion and misinterpretation occur on many levels but include at least the following: 1) confusion of simple allometric truncation and paedomorphosis owing to time and/or rate hypomorphosis with true neotenic paedomorphosis; 2) conflation and equation of prolonged (slowed) growth in time with fundamental neotenic dissociations and shape retardations; 3) acceptance of superficial and non-homologous similarities between human adults and primate juveniles as primary evidence for neoteny; and 4) failure to appreciate the extent and significance of non-paedomorphic features in the evolution of the human lineage.

But if it is correct that the neoteny hypothesis is largely, if not totally, a bankrupt concept when it comes to a careful analysis of human development and evolution, how can we account for its persistent popularity and repeated invocations at the hands of highly qualified specialists? How are we to reconcile the praise and utilization of the general theoretical structure of heterochrony as developed in a modern context by one of our leading evolutionary biologists, S.J. Gould, with a rejection of the bulk of one of his favorite and most detailed case studies? Here we must behave as anthropologists in a broader sense, and recall that in discussions of human neoteny we are not only the administrators of the investigation, but also the subjects of that analysis. Human evolution is, after all, our own pedigree and history. Scholars often fervently hope that their models and theories will fit for this particular lineage above all others. There are many examples where biologists and other scientists have sought to provide extra validation and relevance for their particular models and theories by attempting to demonstrate an application to the human realm, be it biological or sociocultural. These are often at least partially unwarranted extrapolations of the original theses, for a variety of complex reasons. Some recent examples that come to mind are the application of Riedl's (1978) ideas on development and morphological integration to human social behavior and organization (Riedl, 1984); the simplistic extension of Thom's (1975) catastrophe theory to human language and behavior; the much-debated direct extrapolation of aspects of behavioral biology and sociobiology (Wilson, 1975) to human cultural behavior (Wilson, 1978); and perhaps even the disproportionate focus on human evolution by advocates of punctuated equilibrium as the predominant tempo and mode of evolutionary change (Gould and Eldredge, 1977; Eldredge, 1985). Quite simply, I believe this factor accounts for much of the ill-advised concentration on human neoteny as a primary case study of heterochrony over the past century. However, as physical anthropologists and primatologists, we should not make the grave error of concluding that the theory and other primary examples of heterochrony are therefore equally suspect. Gould's (1977) provocative synthesis, as well as McKinney's (1988) recent edited collection (plus extensive citations in both of these works), provide ample documentation of the relevance and vigor of the analysis of heterochrony in evolutionary morphology.

An additional error of interpretation that has proven equally seductive in the debate over human neoteny is the notion that there exists one pervasive key (be it developmental or selective) to the divergence and evolution of our lineage. While such an interpretation may characterize the differentiation of two so similar species as the pygmy and common chimpanzees discussed above, our own evolutionary history has undoubtedly been far too complex to yield to so simple a scenario. This is not a reflection of blatant anthropocentrism but merely the expected result for such an extremely derived organism as *Homo sapiens.*

It will be interesting to see where the neoteny hypothesis of human evolution stands after the next several decades and following the collection of more data in the areas discussed in this paper. My assessment is that physical anthropologists in general will view neoteny as a concept that has contributed more in the way of obfuscation than clarification to the analysis of the processes and patterns of evolutionary change in the human lineage.

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